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Revision of genus *Texoreddellia* Wygodzinsky, 1973 (Hexapoda, Zygentoma, Nicoletiidae), a prominent element of the cave-adapted fauna of Texas

LUIS ESPINASA[1], NICOLE D. BARTOLO[1], DANIELLE M. CENTONE[1],
CHARISSE S. HARUTA[2] & JAMES R. REDDELL[3]
[1]*School of Science, Marist College. Poughkeepsie, New York, USA. E-mail:luis.espinasa@marist.edu*
[2]*Our Lady of Lourdes High School. Poughkeepsie, New York, USA*
[3]*210 Washington St., Killeen, TX 76541*

Abstract

While many cave-adapted organisms tend to be endemic to single locations or restricted to single karstic regions, the troglobitic silverfish insects of genus *Texoreddellia* can be found in scores of different cave localities that cover a range of nearly 160,000 km^2. They are among the most important and common representatives of the cave-adapted fauna of Texas and Coahuila, in northern Mexico. Using morphological and mitochondrial gene sequence data, we have corroborated the presence of at least six different species within the genus and provided species identifications to populations inhabiting 153 different cave locations. Results show that species ranges are larger than previously reported and that ranges tend to greatly overlap with each other. We have also found that different species of *Texoreddellia* commonly inhabit the same cave in sympatry. Data supports that some species of *Texoreddellia* can easily disperse through the extensive network of cracks, fissures and smaller cavities near the surface and epikarst.

Key words: Thysanura, cave, troglobite, biogeography, karst, epikarst, sympatry, biogeography, dispersion

Introduction

Silverfish (Zygentoma) are among the most intriguing of insects. Their predecessors are considered among the earliest, most primitive insects and among the first arthropods to colonize terrestrial habitats. They evolved possibly as early as the late Silurian more than 400 million years ago, having diverged before the appearance of wings in other Insecta (Grimaldi & Engel, 2005). Within the Zygentoma, members of Nicoletiidae typically are adapted to live underground, and lack pigment and eyes. They are intrinsically interesting because of their specialized ecology, but their study has been greatly hampered by the scarcity of locations in which each species can be found. In most cases, species tend to be endemic to single locations and in many cases, species have been described from just a handful of specimens (Espinasa *et al.* 2011).

Members of *Texoreddellia* Wygodzinsky, 1973 (Figs. 1, 2) are an exception. Detailed surveys conducted mostly by James Reddell and colleagues have shown that *Texoreddellia* can be found in myriad cave localities throughout Texas. They are among the most important and common representatives of the cave-adapted fauna of Texas (Reddell, 1994) and Coahuila State in northern Mexico (Espinasa & Giribet 2009). Caves in which *Texoreddellia* spp. have been collected cover an area of nearly 160,000 km^2. Regrettably, only a handful of populations have been properly studied and assigned to a species within the genus. Samples in hundreds of vials, hosted primarily in the Texas Natural History Collections at The University of Texas at Austin (previously Texas Memorial Museum), await study and basic species identification. The purpose of this study is to catalog these specimens, provide species identifications when possible, and conduct a revision of genus *Texoreddellia* using morphologic and DNA data.

Ulrich (1902) described a troglobitic nicoletiid, *Nicoletia texensis*, from Ezell's Cave, in Texas. Wygodzinsky (1973) examined material from this and over a dozen other Texan caves and established a new genus for this species, renaming it *Texoreddellia texensis*. Espinasa and Giribet (2009) examined samples from 25 localities and

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sequenced the 16S rRNA from 17 specimens. Their DNA analyses identified seven phyletic lines. Four of these lines received species recognition, but members of the three remaining lines, despite careful examination, remained mostly qualitatively uniform in their morphology. Espinasa & Giribet (2009) recommended that these three phyletic lines be identified as belonging to the "*T. texensis* species complex". Additionally, two more populations from which DNA data were unavailable received species recognition due to their drastically different morphology. In total, six species were defined: *T. coahuilensis* Espinasa & Giribet, 2009, *T. media* Espinasa & Giribet, 2009, *T. aquilonalis* Espinasa & Giribet, 2009, *T. texensis* species complex, *T. occasus* Espinasa & Giribet, 2009, and *T. capitesquameo* Espinasa & Giribet, 2009 (Fig. 2). The last two species are those not characterized molecularly in the 2009 study.

While most troglobites have small geographical distributions, restricted to limited areas or even to a single cave system (Trajano, 2005), Espinasa & Giribet (2009) found that some *Texoreddellia* species have a wide geographic range and that specimens from neighboring localities can be distantly related. Since biogeography is of little help to assign species identification to the specimens collected in hundreds of different caves, a major revision of the genus is overdue.

Material and methods

Molecular data. Molecular data analyses were completed for 54 individuals from 38 distinct caves (Table 1). Localities from which more than one specimen was sequenced are as follows: two specimens from O-9 Well, two from Seven Mile Mountain Cave, two from Karst Feature 151-018, two from Karst Feature 151-015, two from Karst Feature 151-017, two from Karst Feature HH-2-C, three from Flach's Cave, three from Accident Sink, and four from Ezell's Cave (genus and T. texensis type locality). DNA analyses included the 17 sequences previously obtained by Espinasa & Giribet (2009). The 37 new specimens used for DNA analyses were selected based on date of collection (preferentially less than five years old) so as to reduce extent of DNA degradation. Specimens were also selected for their relevance in resolving taxonomic issues. Therefore, DNA data do not represent a random sample of cave localities and no relative species abundance should be extrapolated from this source. Specimens included both males and females in various stages of post-embryonic development. Genomic DNA samples were obtained from ethanol-preserved tissues following standard methods for DNA purification (Espinasa et al. 2007). Total DNA was extracted with Qiagen's DNeasy Tissue Kit, by digesting one leg of the individual in the lysis buffer. Markers were amplified and sequenced as a single fragment using the 16Sa and 16Sb primer pair for 16S rRNA (Edgecombe et al. 2002). Amplification was carried out in a 50 µL volume reaction, with QIAGEN Multiplex PCR Kit. The PCR program consisted of an initial denaturing step at 94 ºC for 60 sec, 35 amplification cycles (94 ºC for 15 sec, 49 ºC for 15 sec, 72 ºC for 15 sec), and a final step at 72 ºC for 6 min in a GeneAmp® PCR System 9700 (Perkin Elmer).

PCR-amplified samples were purified with the QIAquick PCR Purification Kit and directly sequenced by SeqWright Genomic Services. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher 3.0. All external primers were excluded from the analyses. Sequences were aligned using Clustal Omega. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0 was used to obtain a parsimony bootstrap consensus tree.

Morphology. Samples included all of the Texoreddellia specimens available from the Texas Natural History Collections, for a total of about 500 vials. About half of the vials (Tables 1–3) included specimens amenable for species identification (undamaged adult females). Observations were made with the aid of a Motic-K series stereomicroscope. Measurements were made with the aid of a camera lucida attached to the stereomicroscope. The following information was recorded, preferably from the largest female available in the vial with no severe damage, although in some cases more than one individual was measured: sex, body length, ovipositor/stylet IX length ratio, number of annuli of gonapophysis, hind tibia length/width ratio, penultimate article of the labial palp length/width ratio, and terminal to penultimate articles length ratio. Species names were assigned to the specimens in the vial following the taxonomic key of Espinasa & Giribet (2009), with modifications based on the results of this study (see below). In some vials it was recognized that more than one species of Texoreddellia had been collected. In those cases, measurements were recorded from representative females of both species. Measurements were also obtained from specimens used for DNA analyses prior to removal of a leg for amplification of genomic DNA.

TABLE 1. Cave locality and morphologic measurements of specimens from which 16S rRNA was sequenced. Juvenile measurements, highlighted with an asterisk (*), were not included in the ranges since only adults are used in the taxonomic keys. Empty cellblocks indicate that the measurement could not be obtained because the ovipositor and gonapophyses are only present in females or because the structure was damaged in the specimen.

Clade 1, Group 1: *T. coahuilensis*

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
1	USA, TX, San Saba Co., Colorado Bend State Park, Lemons Ranch Cave, 13 Mar. 2012, #72851	♂ Juvenile	8*	--	--	5*	5.1*	1*
2	Mexico, Coahuila, Acuña, Cueva de Casa Blanca, 19 Feb. 2005	♂	10	--	--	4.3	4.3	1
3	USA, TX, Crockett Co., 0-9 Well, 25 Oct. 2008, #72903	♀	13.5	1.5	14	5.9	5.5	1
4	USA, TX, Crockett Co., 0-9 Well, 19 Jun. 2010, #80150	♀	14.5	1.2	14	4.1	4.6	1
5	USA, TX, Bexar Co., Green Mountain Road Cave, 6 Aug. 2010, #81408	♀	14	1.3	12	4	--	--
		Range in Adults:	**10 – 14.5**	**1.2 – 1.5**	**12 – 14**	**4 – 5.9**	**4.3 – 5.5**	**1**

Clade 1, Group 2: *T. texensis* species complex

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
6	USA, TX, Real Co., Bradford Cave, 22 May 2011, #81196	♂	15	--	--	4.5	--	--
7	USA, TX, Real Co., Red Arrow Cave, 12 Mar. 2005, #37698	♀	13.5	1.1	12	6.1	--	--
8	USA, TX, Edwards Co., Sky High Cave, 3 Sep. 2005, #43563	? (broken)	--	--	--	--	9.7	1.3
		Range in Adults:	**13.5 - 15**	**1.1**	**12**	**4.5 – 6.1**	**9.7**	**1.3**

Clade 1, Group 3: *T. media*

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
9	USA, TX, Bexar Co., Surprise Pit, 28 Mar. 2011, #73624	♀	10	2	14	4.8	5	1
10	USA, TX, Bexar Co., Karst Feature 151-018, 13 Aug 2013, #81492	♂	9	--	--	4.1	--	--
11	USA, TX, Bexar Co., Karst Feature 151-016, 24 Aug. 2012, #81497	♀	11	2	14	4.5	3.8	--
12	USA, TX, Bexar Co., Karst Feature 1609-281 (HH-2-C), 23 Nov 2011, #81558	♂	11.5	--	--	4.6	4.5	1
13	USA, TX, Bexar Co., Karst Feature 151-015, 16 Aug. 2012, #81531	♀	10.5	1.75	14	4.5	--	--
14	USA, TX, Bexar Co., Karst Feature 151-015, 16 Aug. 2012, #81532	♀	11	1.8	14	4.9	3.1	1
15	USA, TX, Bexar Co., Karst Feature 151-017, 13 Aug 2012, #81505	♀	10	--	--	4.6	--	1
16	USA, TX, Bexar Co., Karst Feature 151-018, 17 Aug 2013, #81502	♀	11.5	--	14	--	--	--
17	USA, TX, Bexar Co., Karst Feature 151-017, 17 Aug. 2012, #81509	♀	8.5	--	14	4.2	4.2	1
18	USA, TX, Bexar Co., Flach's Cave, 23 Feb. 2008, #69366	♀	14	2	14	4	5.3	1
19	USA, TX, Bexar Co., Accident Sink, 9 May 2005, #38098	♀	15	1.7	14	4.8	5.1	1
20	USA, TX, Bexar Co., Flach's Cave, 7 Dec. 2004, #37377	♀	11	1.8	14	--	4.1	1
21	USA, TX, Bexar Co., Accident Sink, 9 May 2005, #38098	♀	14	1.6	14	--	5.2	1
22	USA, TX, Bexar Co., Karst Feature 1609-281 (HH-2-C), 23 Nov 2011, #81558	♀	10.5	1.75	15	5	5.3	1.1
23	USA, TX, Bexar Co., Taco Truck Hole, 17 Sep. 2010, #75244	♀	9	2	15	5	4.7	1
24	USA, TX, Bexar Co., Green Mountain Road Cave, 6 Aug. 2010, #81403	♀	--	1.75	14	5.1	4.6	1
25	USA, TX, Comal Co., Echo River Cave, 2 Jan. 2006, #49710	♀	12.5	2.1	14	4.5	4.9	1
		Range in Adults:	**9 - 15**	**1.6 – 2.1**	**14 – 15**	**4.1 – 5.1**	**3.1 – 5.3**	**1 – 1.1**

Clade 1, Group 4: *T. texensis* species complex

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
26	USA, TX, Bell Co., Mixmaster Cave, 8 Dec. 2007, #61526	♂ Juvenile	6*					
27	USA, TX, Travis Co., Flint Ridge Cave, 11 Jan. 2005	♀	9	0.9	12	--	9.5	1.2

Clade 1, Group 5: *T. aquilonalis*

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
28	USA, TX, Williamson Co., Cowan Creekside Cave, 18 Oct. 2010, #75303	♂ Juvenile	8*	--	--	--	3.2*	1*
29	USA, TX, Bell Co., Fort Hood, Seven Mile Mountain Cave, 23 Apr. 2004, #36237	♂	15	--	--	4.4	6.2	1
30	USA, TX, Bell Co., Fort Hood, Seven Mile Mountain Cave, 11 Jun. 2005, #38263	♀ Juvenile	10*	0.33*	17*	3.8*	3.5*	1*
31	USA, TX, Williamson Co., Cobb Cavern, 30 Mar. 2004, #36173	♀	15	2.2	18	5.4	6	1
32	USA, TX, Travis Co., Bomb Shelter Cave (Site 59), 14 Dec. 2007	♀	12.9	2	16	4.9	6	1
33	USA, TX, Travis Co., No Rent Cave, 22 Jul. 2010, #75209	♀ Juvenile	9.5*	0*	--	3.9*	3.6*	1*
34	USA, TX, Williamson Co., Highway 183A, Karst Feature 11, 15 Mar. 2006, #62380	Juvenile	5*	--	--	4.6*	3.1*	1*
		Range in Adults:	**12.9 – 15**	**2 – 2.2**	**16 – 18**	**4.4 – 5.4**	**6 – 6.2**	**1**

Clade 2, Group 6: *T. texensis*

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia WidthRatio	Palp Width Ratio	Palp Segment Ratio
A	USA, TX, Bexar Co., Flach's Cave, 23 Feb. 2008, #69366	♀	13	1.1	12	6.1	9.3	1.4
B	USA, TX, Bexar Co., Camp Bullis, Root Canal Cave, 18 May 2006, #56810	♀	--	--	12	--	--	--
C	USA, TX, Bexar Co., Camp Bullis, Root Canal Cave, 18 May 2006, #56810	♂	--	--	--	--	--	--
D	USA, TX, Bexar Co., Aqualogic Cave, 30 Aug. 2012, #81464	♀	10.5	1	12	6.1	--	--
E	USA, TX, Kendall Co., Spring Creek Cave, 21 Jan 2012, #81381	♀	13	1	12	6.3	7.9	1.3
F	USA, TX, Bexar Co., Hanging Rock Cave, 27 Jun 2011, #75192	♀ Juvenile	5.5*	0*	0*	6.1*	5.3*	--
G	USA, TX, Bexar Co., Camp Bullis, Accident Sink, 12 Apr. 2005	♂	12	--	--	6.4	9.7	1.2
H	USA, TX, Travis Co., Whirlpool Cave, 2 Mar. 2005	♀	11	0.8	12	9.9	13.9	1.4
I	USA, TX, Coryell Co., Formation Cave, Fort Hood, 29 Aug. 2005, #41364	Juvenile	--	--	--	--	--	--
J	USA, TX, Travis Co., Airman's Cave, Unknown date	♂ Juvenile	5*	--	--	10.1*	6.9*	1*
K	USA, TX, Hays Co., Hoskin's Hole, Unknown date	♀	8.5	0.9	12	6.4	--	--
L	USA, TX, Hays Co., Ezell's Cave, 1 Jun. 2006	♂	--	--	--	7.9	9.8	1.2
M	USA, TX, Hays Co., Ezell's Cave, 1 Jun. 2007	♀ Juvenile	--	0*	0*	7.2*	9.4*	1.1*
N	USA, TX, Hays Co., Ezell's Cave, 14 Feb 2006	♂ Juvenile	6*	--	--	5.5*	--	--
O	USA, TX, Hays Co., Ezell's Cave 17 Dec. 2006, #56811	Juvenile	--	--	--	--	--	--
P	USA, TX, Travis Co., Ireland's Cave, 9 Mar. 2005	♂	10.5	--	--	7	10.9	1.5
		Range in Adults:	**8.5 – 13**	**0.8 – 1.1**	**12**	**6.1 – 9.9**	**7.9 – 13.9**	**1.2 – 1.5**

Clade 3, Group 7: *T. texensis* species complex

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
I	USA, TX, Travis Co., Pickle Pit, 5 Apr. 2011 #73661	Juvenile	5*	--	--	3.9*	3.5*	1*
II	USA, TX, Travis Co., Water Treatment Plant 4 Road H, 30 Mar. 2011, #75346	♂	9	--	--	5.5	3.4	1.2
III	USA, TX, Bexar Co., Camp Bullis, Root Canal Cave, 9 Jul. 1998	♀	--	1	12	--	--	--

Clade 4, Group 8: *T. capitesquameo*

#	Locality, Collection Date, TNHC Collection Number (when available)	Sex	Length (mm)	Ovipositor to Stylet IX Ratio	Gonapophysis # of annuli	Tibia Width Ratio	Palp Width Ratio	Palp Segment Ratio
	USA, TX, Reeves Co., Phantom Lake Cave, 13-17 Mar. 2014	♀	9	1	14	6	7.7	1.2

Morphological measurements were obtained from a total of 355 individuals. Species assignments with the help of both DNA and morphology data were made for 54 individuals from 38 cave localities (Table 1). Species assignments for which only morphology data were available included individuals from another 180 vials from 131 different localities (Table 2–3). Since some of the localities overlap, 153 localities received species identification. This number is more than six times the number of localities with assigned species used in the original study of Espinasa & Giribet (2009).

TABLE 2. Cave localities for specimens of the *Texoreddelli. texensis* species complex for which only morphological data were available. TNHC=Texas Natural History Collections.

Country	State	County	Cave	Collection Date	TNHC Number
USA	TX	Bell	Nolan Creek Cave	17 Jul 1993	#24679
USA	TX	Bexar	40 mm Cave	5 Oct 1995	#24713
USA	TX	Bexar	B-52 Cave	31 Mar 1995	#24711
USA	TX	Bexar	Backhole Cave	20 Sep 1994	#24590
USA	TX	Bexar	Banzai Mud Dauber Cave	5 Dec 1994	#24600
USA	TX	Bexar	Banzai Mud Dauber Cave	10 Nov 2000	#26442
USA	TX	Bexar	Bet Ya Can't Breathe Cave	Unknown	N/A
USA	TX	Bexar	Black Cat Cave	27 Jan 1987	#24618
USA	TX	Bexar	Boneyard Pit	5 Dec 1994	#24595
USA	TX	Bexar	Boneyard Pit	7 Sep 1998	#17989
USA	TX	Bexar	Boneyard Pit	11 Oct 2005	N/A
USA	TX	Bexar	Borehole 151 RW1-2	28 Jan 2012	#81466
USA	TX	Bexar	Bunny Hole	31 Mar 1995	#24709
USA	TX	Bexar	Calmbach Cave	Apr 1987	#24637
USA	TX	Bexar	Cave Site #303	Jan 2000	#24708
USA	TX	Bexar	Christmas Cave	6 Sep 1993	#24714
USA	TX	Bexar	Dogleg Cave	25 Mar 1998	#24545
USA	TX	Bexar	Dos Viboras Cave	9 Jan 1995	#24707
USA	TX	Bexar	Eagle's Nest Cave	20 Apr 1999	#17986
USA	TX	Bexar	Elm Springs Cave	12 Aug 1984	#24729
USA	TX	Bexar	Elm Springs Cave	12 Aug 1984	#24704
USA	TX	Bexar	Elm Water Hole Cave	10 May 2000	#18435
USA	TX	Bexar	Flach's Cave	2 Feb 1999	#17993
USA	TX	Bexar	Game Pasture Cave	2 Jun 1993	#24727
USA	TX	Bexar	Hairy Tooth Cave	8 Feb 1987	#24641
USA	TX	Bexar	Hairy Tooth Cave	21 Jan 1994	#24678
USA	TX	Bexar	Headquarters Cave	19 Jun 1993	#24586
USA	TX	Bexar	Headquarters Cave	7 Mar 2006	#56813
USA	TX	Bexar	Hector's Hole	15 Apr 2002	#32731
USA	TX	Bexar	Hector's Hole	7 May 2003	#34565
USA	TX	Bexar	Hills and Dales Pit	Nov 2000	#29533
USA	TX	Bexar	Hold Me Back Cave	3 Mar 1994	#24675
USA	TX	Bexar	Hold Me Back Cave	21 Sep 1994	#24597
USA	TX	Bexar	Hold Me Back Cave	9 Nov 2000	#26423

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TABLE 2. (Continued)

Country	State	County	Cave	Collection Date	TNHC Number
USA	TX	Bexar	Hold Me Back Cave	25 Oct 2001	N/A
USA	TX	Bexar	Hold Me Back Cave	5 Oct 2005	N/A
USA	TX	Bexar	Holy Smoke Cave	7 Mar 2001	#29650
USA	TX	Bexar	Hornet's Last Laugh Pit	3 Jun 2002	#33081
USA	TX	Bexar	Isocow Cave	24 Oct 2005	N/A
USA	TX	Bexar	Isopit Cave	1984	#24587
USA	TX	Bexar	Isopit Cave	8 Jan 1984	#24696
USA	TX	Bexar	Isopit Cave	17 Sep 1984	#24588
USA	TX	Bexar	Kick Start Cave	30 May 2002	#33073
USA	TX	Bexar	Kick Start Cave	6 Jun 2002	#33068
USA	TX	Bexar	King Toad Cave	1 Jun 1993	#24724
USA	TX	Bexar	Larsen's Pit	Unknown	#31443
USA	TX	Bexar	Lithic Ridge Cave	1 Oct 1994	#24728
USA	TX	Bexar	La Cantera Cave No. 1	9 Mar 2005	N/A
USA	TX	Bexar	Logan's Cave	10 May 1992	#24617
USA	TX	Bexar	Logan's Cave	8 Jun 1993	#24723
USA	TX	Bexar	Lost Pot Cave	4 Feb 1995	#24699
USA	TX	Bexar	Madla's Drop Cave	24 May 1993	#24669
USA	TX	Bexar	Madla's Drop Cave	8 Jun 1993	#24719
USA	TX	Bexar	MARS Pit	9 Oct 1995	#24567
USA	TX	Bexar	MARS Pit	10 Sep 1998	#17997
USA	TX	Bexar	MARS Pit	29 Oct 2001	N/A
USA	TX	Bexar	MARS Pit	30 Oct 2001	N/A
USA	TX	Bexar	MARS Shaft	20 Sep 1994	#24592
USA	TX	Bexar	MARS Shaft	25 Oct 2001	N/A
USA	TX	Bexar	Mastodon Pit	30 Feb 2002	#33202
USA	TX	Bexar	Mastodon Pit	Apr 2002	#33196
USA	TX	Bexar	Pain in the Glass Cave	5 Oct 2005	N/A
USA	TX	Bexar	Pig Cave	23 Apr 2002	#33212
USA	TX	Bexar	Platypus Pit	30 Mar 1995	#24552
USA	TX	Bexar	Platypus Pit	24 Oct 2005	N/A
USA	TX	Bexar	Poor Boy Baculum Cave	15 Dec 1994	#24599
USA	TX	Bexar	Poor Boy Baculum Cave	31 Oct 2005	#49744
USA	TX	Bexar	Root Canal Cave	20 Apr 1999	#17985
USA	TX	Bexar	Root Canal Cave	26 Oct 2001	N/A
USA	TX	Bexar	Root Toupee Cave	20 Apr 1999	#17990
USA	TX	Bexar	Stahl's Cave	21 Apr 1998	#25543
USA	TX	Bexar	Stahl's Cave	21 Apr 1999	#17995
USA	TX	Bexar	Stahl's Cave	14 Dec 2000	#29560
USA	TX	Bexar	Strange Little Cave	29 Nov 1993	#24640
USA	TX	Bexar	Strange Little Cave	22 Mar 2004	#36326
USA	TX	Bexar	Ragin' Cajun Cave	Unknown	#31401

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TABLE 2. (Continued)

Country	State	County	Cave	Collection Date	TNHC Number
USA	TX	Bexar	Ragin' Cajun Cave	22 Jan 1994	#23201
USA	TX	Bexar	Robber Baron Cave	11 Dec 1983	#24559
USA	TX	Bexar	Robber Baron Cave	25 Jun 1993	#24620
USA	TX	Bexar	Robber's Cave	22 Jun 1993	#24708
USA	TX	Bexar	Robber's Cave	14 July 1993	#24668
USA	TX	Bexar	Scorpion Cave	1 Jun 1993	#24563
USA	TX	Bexar	Steven's Ranch Trash Hole Cave	12 June 1993	#24676
USA	TX	Bexar	Stien Cave	10 May 2001	#30439
USA	TX	Bexar	Surprise Sink	21 Apr 1996	#24570
USA	TX	Bexar	Surprise Sink	24 May 1998	#24532
USA	TX	Bexar	Three-Fingers Cave	22 June 1993	#24726
USA	TX	Bexar	Winston's Cave	1 Feb 1994	#24695
USA	TX	Bexar	Winston's Cave	21 Sep 1994	#24594
USA	TX	Bexar	Winston's Cave	13 Nov 2000	#29842
USA	TX	Comal	Bain's Cave	19 July 1987	#24636
USA	TX	Comal	Cactus Crack	Jan 2003	#33537
USA	TX	Comal	Just Now Cave	14 Nov 1996	#24531
USA	TX	Comal	Just Now Cave	21 Nov 2006	#24542
USA	TX	Comal	Kuhn's Ranch, 70 Footer Cave	22 Aug 2005	#73215
USA	TX	Comal	Little Bear Creek Cave	20 Aug 1988	#24609
USA	TX	Comal	Natural Bridge Caverns	23 Sep 1989	#24742
USA	TX	Hays	Dahlstorm Cave	2 Apr 2009	#70645
USA	TX	Hays	Halifax Ranch, 6F Cave	7 May 2009	#70646
USA	TX	Hays	Halifax Ranch, 6F Cave	7 May 2009	#70696
USA	TX	Hays	Jagarundi Cave	5 Sept 2014	#89457
USA	TX	Hays	Lime Kiln Quarry Cave	21 Apr 1992	#24666
USA	TX	Hays	McCarty Cave	14 Mar 2000	#18004
USA	TX	Hays	Pulpit Cave	30 Aug 2009	#70650
USA	TX	Kendall	Sattler/Hoffman Ranch, Peanut Cave	11 Mar 2006	#50314
USA	TX	Kendall	Sattler/Hoffman Ranch, Peanut Cave	11 Mar 2006	#50313
USA	TX	Kendall	Spring Creek Cave	26 Oct 2008	#69872
USA	TX	Kendall	Hal's Cave	4 Mar 1999	#18002
USA	TX	Kendall	Day After Cave	7 Jan 1989	#24660
USA	TX	Kendall	Day After Cave	16 Feb 1984	#24682
USA	TX	Kendall	Pfeiffer's Water Cave	7 Nov 1992	#24583
USA	TX	Kendall	Sattler's Deep Pit	10 Jul 1994	#24537
USA	TX	Kendall	Sattler's Deep Pit	28 Apr 1990	#24661
USA	TX	Kendall	Knee Deep Cave	9 Aug 1984	#24739
USA	TX	Medina	Boehme's Cave	19 Oct 2007	#62396
USA	TX	Medina	Marguerite Cave	28 Apr 1984	#24576
USA	TX	Medina	Marguerite Cave	5 May 1984	#24736
USA	TX	Medina	Worm Hole	4 Mar 2001	#29639

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TABLE 2. (Continued)

Country	State	County	Cave	Collection Date	TNHC Number
USA	TX	Terrell	Sorcerer's Cave	22 Sep 2001	#31372
USA	TX	Terrell	Sorcerer's Cave	28 Sep 2002	#33225
USA	TX	Travis	Bandit Cave	13 Sep 1988	#24623
USA	TX	Travis	Cave X	15 Jun 1996	#24575
USA	TX	Travis	Cave Y	14 June 1990	#24649
USA	TX	Travis	Cortaña Feature	25 Sep 2007	#61443
USA	TX	Travis	Flint Ridge Cave	8 Jun 1984	#24681
USA	TX	Travis	Flint Ridge Cave	19 Jan 1989	#24653
USA	TX	Travis	Flint Ridge Cave	21 Jan 1989	#24734
USA	TX	Travis	Flint Ridge Cave	22 Dec 1999	#19249
USA	TX	Travis	Ireland's Cave	25 Jan 1986	#24580
USA	TX	Travis	Karst Feature F10	4 Oct 2006	N/A
USA	TX	Travis	Maple Run Cave	Oct 1983	#24648
USA	TX	Travis	Slaughter Creek Cave	3 Mar 1990	#24654
USA	TX	Travis	Whirlpool Cave	22 Oct 1988	#24621
USA	TX	Uvalde	Barn-Sized Fissure Cave	17 Mar 1993	#24528
USA	TX	Val Verde	Seminole Canyon Cave	Jul 1984	#24743
USA	TX	Williamson	Hidden Corner Cave	22 May 2006	#50325

TABLE 3. Cave localities for *Texoreddellia* spp. other than *T. texensis* for which only morphological data were available. TNHC=Texas Natural History Collections.

Country	State	County	Cave	Collection Date	TNHC Number
T. capitesquameo					
USA	TX	Reeves	Phantom Lake Cave	Jul 1997	#24535
T. aquilonalis					
USA	TX	Bell	Seven Mile Mountain Cave	11 Apr 1999	#24752
USA	TX	Bell	Seven Mile Mountain Cave	28 Jun 2000	#20484
USA	TX	Medina	Marguerite Cave	28 Apr 1984	#24576
USA	TX	Travis	Highway 183 Karst Feature 2: Chapman Cave	1 Nov 2005	#62425
USA	TX	Travis	State Well Number 58-50-705	2015	Zara-9008
USA	TX	Travis	Wade Sink	2013	83976
USA	TX	Travis	No Rent Cave	11 Jun 1990	#24622
USA	TX	Williamson	On Campus Cave	7 May 1992	#24616
USA	TX	Williamson	Polaris Cave	19 Apr 1994	#24684
USA	TX	Williamson	Highway 183A: Karst Feature 11	15 Jun 2006	#30441
T. occasus					
USA	TX	Ward	Rattlesnake Cave	12 May 1986	#24635
T. coahuilensis					
USA	TX	Bexar	Power Pole 60 Feature	30 Apr 2003	#34580
USA	TX	Crockett	O-9 Well	15 Aug 1992	#24730
USA	TX	Crockett	O-9 Well	29 Sept 2007	#62431
USA	TX	Travis	Ireland's Cave	1 Mar 1986	#24579

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TABLE 3. (Continued)

Country	State	County	Cave	Collection Date	TNHC Number
USA	TX	Val Verde	Emerald Sink	31 Mar 1984	#24556
MX	COA	Acuña	Sotano de Amezcua	14 Nov 1992	#23584
MX	COA	Acuña	Sotano de Amezcua	26 Jun 1994	#25585
MX	COA	Acuña	Sotano de Amezcua	27 Jun 1994	#23756
MX	COA	Acuña	Sotano de Amezcua	15 Jun 1998	#23583
MX	COA	Arteaga	Grutas de Arteaga	18 Aug 2006	
T. media					
USA	TX	Bexar	50 Bucket Cave.	7 Feb 2008	#64953
USA	TX	Bexar	Bunny Hole	24 Oct 1995	#24554
USA	TX	Bexar	Accident Sink	26 Oct 2004	#37387
USA	TX	Bexar	Hector's Hole	15 Apr 2002	#32731
USA	TX	Bexar	Caracol Creek Coon Cave	15 June 1993	#24673
USA	TX	Bexar	Elm Springs Cave	Unknown	#31531
USA	TX	Bexar	Green Mountain Road Cave	17 Sep 2010	#72513
USA	TX	Bexar	Karst Feature 115-010	16 Jul 2012	#81470
USA	TX	Bexar	Karst Feature 115-014	13 Aug 2012	#81493
USA	TX	Bexar	Karst Feature 281-080	11 Jun 2010	#71089
USA	TX	Bexar	Karst Feature 281-080	17 Jun 2010	#71072
USA	TX	Bexar	Karst Feature 281-080	17 Jun 2010	#71052
USA	TX	Bexar	Robber Baron Cave	11 Dec 1983	#24559
USA	TX	Menard	Powell's Cave	23 Oct 1993	#24731
USA	TX	Travis	Fossil Garden Cave	6 Jun 1990	#24652
USA	TX	Travis	Sunset Valley Cave	29 Aug 1993	#24655
USA	TX	Travis	Ulls Water Cave	27 Apr 2000	#19402
USA	TX	Williamson	Buttercup Creek Cave	16 Feb 1991	#24629
USA	TX	Williamson	Pomegranate Pit	1 Oct 1991	#24613
USA	TX	Williamson	Water Tank Cave	29 Oct 1998	#17999
USA	TX	Williamson	Sunchase Cave	10 Aug 1998	#17998
USA	TX	Williamson	Rim Rock Ledge Cave	18 Mar 1993	#24748

Results

Molecular results. Molecular data were obtained for 54 individuals from 38 cave localities (Table 1). The 16S rRNA fragment ranged between 497 and 501 bp for all specimens, with the exception of a specimen of T. capitesquameo from Phantom Lake Cave (Fig. 2), which was distinctly longer, 519 bp, due to an insertion of about 20 bp at the 5' end of the fragment (GenBank# KU711930). Excluding this individual, alignment through Clustal Omega was trivial and involved insertion/deletions in only 7 positions. Espinasa & Giribet (2009) divided Texoreddellia into seven groups among three major clades, based on DNA analyses of 17 specimens. These groups were assumed to be correlated with species delimitations, although three were defined as "T. texensis species complex" because they did not have differentiating diagnostic morphologic characters. Our tree, based on 54 specimens, yielded the same three clades with all the specimens fitting well within the seven previously defined groups (Fig. 3), plus the extra T. capitesquameo individual which added a new, most basal clade. This arrangement corroborates the previous conclusion of Espinasa & Giribet (2009), based exclusively with morphology, that T.

capitesquameo and T. occasus are phylogenetically the sister species of the eastern groups and the most basal clades within the Taxoreddellia species.

Sequence divergence among the populations ranged from zero to 103 bp (0–19.84%; Table. 4). Several specimens from different localities had the same haplotypes. From Clade 1, the specimens from Sky High Cave in Edwards County shared haplotypes with those of Red Arrow Cave and Bradford Cave from neighboring Real County. Seven Mile Mountain Cave specimens from Fort Hood, Bell County, shared haplotypes with those from Cobb Cavern and Cowan Creekside Cave, in neighboring Williamson County. Bomb Shelter Cave and No Rent Cave, both from Travis County, shared a haplotype, as did Flach's Cave and Karst Feature 151-017 from Bexar County. The same haplotypes could also be found in specimens from Clade 2 even when separated by long distances. Specimens from Formation Cave from Fort Hood (Coryell County), Airmans Cave (Travis County), Whirlpool Cave (Travis County), and Hoskin's Hole (Hays County) showed no sequence divergence and only a single nucleotide difference was found with the four specimens from Ezell's Cave (Hays County), the type locality of *T. texensis*. Specimens from Bexar County (Flach's Cave, Root Canal Cave, Aqualogic Cave, Hanging Rock Cave, and Accident Sink) and Kendall County (Spring Creek Cave) also had no sequence differences. Finally, from Clade 3, Pickle Pit and Water Treatment Plant 4 Road H Void, both from Travis County, shared the same haplotype.

Comparison of the 16S rRNA tree (Fig. 3) with the type of ovipositor and length of appendages (Table 1) yielded a phylogenetic pattern that is mostly concordant with the species diagnostic characters proposed by Espinasa & Giribet (2009). In a few cases the structures of some specimens were slightly outside the range of their original species definition, and only minor adjustments to the respective species definitions were needed to include these outliers. Therefore, modifications of some species diagnoses are given as follows.

Texoreddellia coahuilensis. This species was defined as having an ovipositor surpassing the tips of stylets IX by about 1/10 their length in adult females, gonapophysis with about 12 annuli, and a range restricted to Mexico, south of the Rio Grande. Tree topology showed individuals within this phyletic group to have an ovipositor surpassing the tips of stylets IX by up to half their length in adult females, gonapophysis with about 12–14 annuli, and a range including San Saba, Crockett and Bexar Counties in Texas.

FIGURE 1. Live specimen of *Texoreddellia* sp. Body length 12 mm. Photograph reproduced with permission of William R. Elliot.

FIGURE 2. Live specimen of *T. capitesquameo* from Phantom Lake Cave. DNA sequence confirmed that the western species are phylogenetically the sister species of the Eastern groups and the most basal clades within the *Taxoreddellia* species. Photograph reproduced with permission of Dr. Jean K. Krejca, Zara Environmental LLC.

Texoreddellia media. Espinasa & Giribet (2009) included within this species populations that were highly dissimilar with respect to ovipositor length. Included within this species were specimens from Flach's Cave (12 mm) and Accident Sink (14, 15, 15 mm), whose ovipositor surpassed the tip of stylets IX by about half their length; a specimen from Robber Baron Cave (13 mm) whose ovipositor surpassed the tip of stylets IX by a distance equal to a stylet length; and two specimens from 0-9 Well (12, 15 mm) whose ovipositor surpassed the tips of stylets IX by only 1/3 their length. The new DNA sequences showed that the O-9 Well specimens actually belong within *T. coahuilensis*. Therefore, the limits of *T. media* are now corrected to include only those adult females that have an ovipositor surpassing the tips of stylets IX by more than half their total length, which excludes the O-9 well population.

Texoreddellia capitesquameo. Espinasa & Giribet (2009) described this species based on only two specimens, a 7-mm-long male and an 11-mm female. They noticed that the relative length of mouthparts was dissimilar in these two specimens. In this study two new females were examined (9 and 15 mm; Fig. 2) and they also showed dissimilar morphology. The smaller individual has an ovipositor that surpasses the tip of stylets IX by the length of the stylets and the gonapophyses has 14 annuli. The larger individual has broken stylets IX, but it is estimated that it would surpass them by about 1.5× their length, and the gonapophysis has 18 annuli. Such a difference would be expected if they belonged to two different species. The largest specimens of the two species in western Texas, *T. capitesquameo* (11 mm) and *T. occasus* (11.5 mm), have 14 or 15 annuli, but since the 15-mm-long new individual is larger than either previously described specimens, it is unclear if the difference is due only to postembryonic development or the presence of a previously undescribed species. In conclusion, it appears that Phantom Lake cave may be inhabited by two different species. DNA sequences could resolve this issue but regrettably only the smallest specimen could be successfully sequenced.

Texoreddellia aquilonalis*, *T. texensis,* and *T. occasus. The diagnostic morphology of these species was not changed even with the addition of more specimens from a greater geographic range of caves.

TABLE 4. Sequence divergence among the populations. Percentages are given from the aligned sequences. The 16S rRNA fragment ranged between 497 and 519 bp in the specimens sequenced. For comparison of individual pairs of samples, sequence differences ranged from zero to 103 bp.

		Clade 1					Clade 2	Clade 3	Clade 4
		Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
		T. coahuilensis	*T. texensis* species complex	*T. media*	*T. texensis* species complex	*T. aquilonalis*	*T. texensis*	*T. texensis* species complex	*T. capitesquameo*
Clade 1	Group 1	0–2.0%							
	Group 2	4.1–5.7%	0%						
	Group 3	3.6–5.6%	3.6–4.6%	0–2.4%					
	Group 4	4.7–6.1%	4.9–5.1%	2.4–3.4%	0–1.2%				
	Group 5	4.0–5.5%	3.8–4.1%	1.6–2.8%	2.8–3.3%	0–0.4%			
Clade 2	Group 6	7.0–9.6%	7.6–8.4%	7.4–9.4%	8.2–9.2%	8.2–9.8%	0–2.6%		
Clade 3	Group 7	7.8–9.0%	9.0–9.6%	9.0–10.4%	9.8–10.6%	9.0–9.8%	5.8–6.4%	0–1.6%	
Clade 4	Group 8	18.4–19.0%	19.6%	18.8–19.4%	19.4–19.8%	19.0–19.2%	18.3–18.4%	16.7%	0%

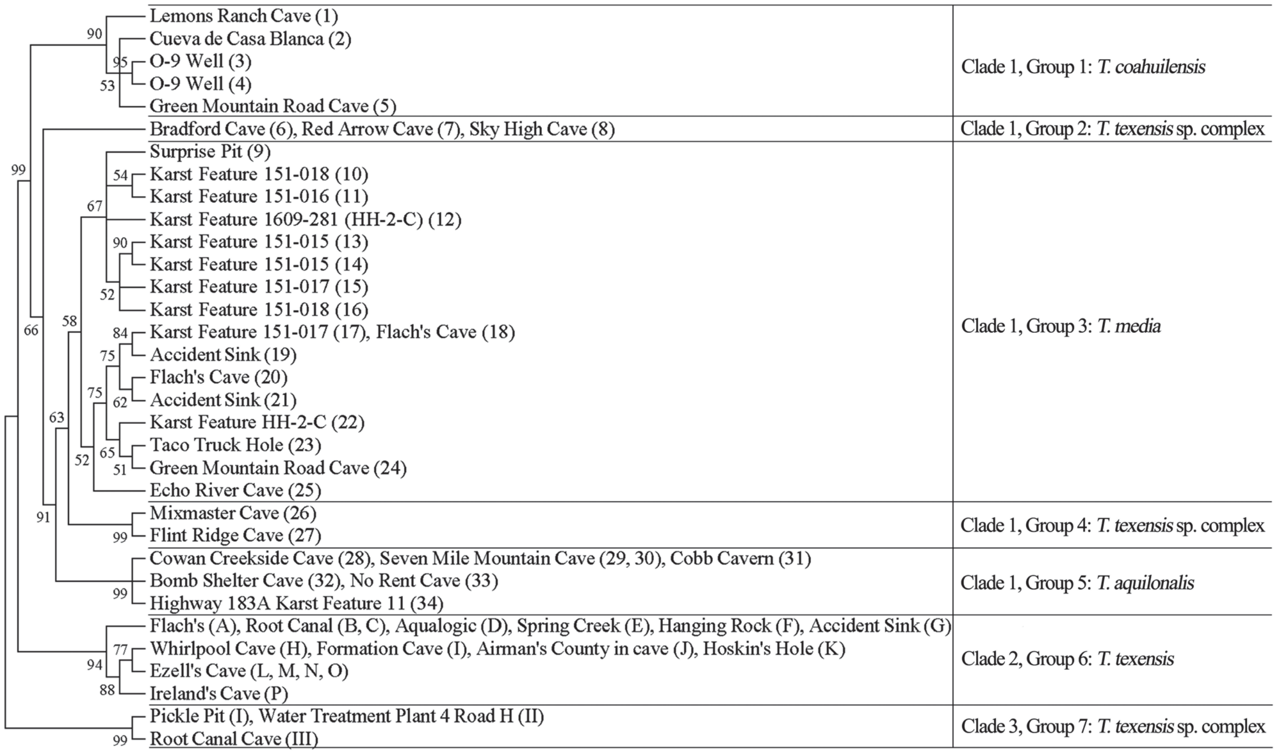

FIGURE 3. Parsimony bootstrap consensus tree. *Texoreddellia capitesquameo* from Phantom Lake Cave (Clade 4, Group 8) as outgroup is not shown. Branches where more than one cave locality are included indicate that they had identical DNA sequences in their 16S rRNA. Individuals within each of the seven groups are concordant to a particular morphology.

Postembryonic development. Espinasa and Giribet (2009) provided a table of the postembryonic development for the different species of *Texoreddellia*. This table included specimens assigned to a species based exclusively on morphology. Our DNA results show that some of these specimens were incorrectly assigned (O-9 Well). With the new samples assigned to different species (Table 1), as supported by both DNA and morphology, the most prominent result from the postembryonic development analysis is that different species, apart from differing in their adult morphology, also differ in their development. While most species tend to reach an adult morphology when they have attained a body length of 8–9 mm, in *T. aquilonalis* adults are 10-13 mm long.

Biogeography. The nearly six-fold increase in available samples over those available to Espinasa & Giribet (2009) resulted in expanded known ranges for the various species (Fig. 4). The most significant increase was for *T. coahuilensis*, previously thought to be restricted to Mexico. It is now clear that it also has a wide distribution throughout most karstic areas of Texas (Fig. 4C).

Espinasa & Giribet (2009) reported that the *Texoreddellia* species phyletic groups followed a biogeographical pattern where species are positioned with a somewhat east-west distribution, with *T. aquilonalis* populations on the northeastern edge of the karstic region of Texas (Bell, Williamson, and Travis counties), *T. media* more southwest (Comal and Bexar Counties), *T. coahuilensis* even further west (Bexar, San Saba, Crockett counties in Texas and Coahuila, in Mexico), ending with *T. occasus* (Ward County) and *T. capitesquameo* (Reeves County) on the western end of Texas. In our enlarged sample, species ranges greatly overlap with each other (Fig. 4), resulting in the trend being somewhat obscured, highlighting that caution should be used when interpreting this trend.

Espinasa & Giribet (2009) also found that some individual caves were inhabited by more than one species of *Texoreddellia*. This conclusion was supported by only three DNA sequences. In Accident Sink in Camp Bullis (Bexar County), females collected on 26 October, 2004 and on 12 April, 2005, had long appendages and short ovipositors with about 12 annuli. The 16S rRNA sequence of one of these specimens indicated that it belonged to *T. texensis*. However, a collection from the same cave at a later date (May 9, 2005) yielded specimens with short appendages and long ovipositors with about 14 annuli. Based on 16S rRNA sequences, two May 9 specimens were identified as *T. media*. Our results support the conclusion of Espinasa & Giribet (2009) that *Texoreddellia* spp. can be sympatric. Specimens collected from Green Mountain Road Cave (Bexar County) on August 6, 2010, had a

mixture of long and short ovipositors. DNA sequences showed that they belonged to *T. media* and *T. coahuilensis*, respectively. Likewise, morphology and DNA of a specimen collected from Flach's Cave (Bexar County) on December 7, 2004, indicated that it was *T. media*, but a pair of specimens collected on February 23, 2008, belong to two different species, *T. media* and *T. texensis*. Finally, a specimen from Root Canal Cave (Bexar County) collected on July 9, 1998, belonged to *T. texensis* species complex Clade 3, group 7, while two specimens collected on May 18, 2006, belonged to *T. texensis* Clade 2, group 6.

Apart from the four cave localities where DNA supported the presence of more than one species at one time or another, based on morphology alone there are six additional localities where two species may be in sympatry. Specimens from several Bexar County caves (Bunny Hole, Elm Springs Cave, Hector's Hole, Robber Baron Cave), Medina County (Marguerite Cave) and Reeves County (Phantom Lake Cave) had morphological evidence of sympatry.

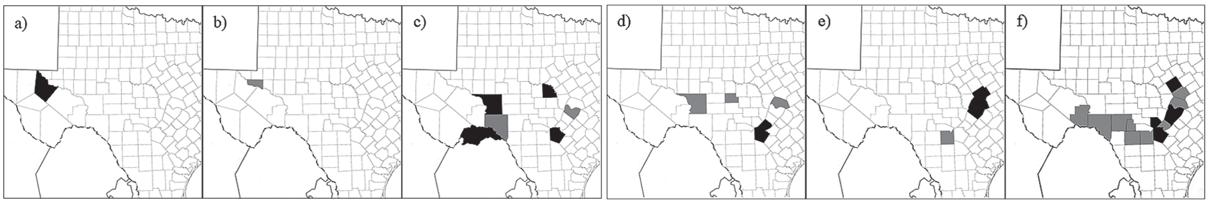

FIGURE 4. Known geographic ranges of *Texoreddellia* spp. by county. a) *T. capitesquameo*; b) *T. occasus*; c) *T. coahuilensis*; d) *T. media*; e) *T. aquilonalis*; f) *T. texensis*. Areas shaded in black are counties in which DNA sequencing confirmed species identification. Areas shaded in gray are counties in which species identity has been determined solely through morphological analysis.

Discussion

Monophyly of *Texoreddellia* was supported by the results. Molecular relationships within *Texoreddellia* appear to subdivide the group into four major clades. One of these clades can be further divided into five subgroups (Fig. 3) to give eight apparent taxa. It is likely that these eight groups are equivalent to species, although three of them lack recognizable and diagnostically unique morphological characters (Table 1). Following Espinasa & Giribet (2009), we do not feel it is suitable to designate different species based solely on haplotypes, especially when considering the limited information available for study. There is one additional species from western Texas, *T. occasus*, for which DNA data are not available. We have no reason to disagree with Espinasa & Giribet (2009) that this species is closely related to *T. capitesquameo* and a sister group to the eastern clades.

Taxonomy. Based on the results from this study, the species key of Espinasa and Giribet (2009) has been modified. Characters are based on adult specimens that are typically over 9 mm long and can be recognized as females by possession of a gonapophysis, including its distal portion, clearly subdivided into annuli. Since juvenile females have smaller ovipositors and the length of the ovipositor is one of the diagnostic features for species recognition, we recommend that after using the following key, Table 1 should be reviewed to assure proper species identification. Figures referenced are from Espinasa & Giribet (2009).

Key to *Texoreddellia* spp.

1. Pedicellus projection in adult males blade-like, not very conspicuous, extending parallel to antennae. Length of the projection shorter than one third the length of pedicellus (Figs. 4B–D, 6B–C and 9C–D) 2

\- Pedicellus projection in adult males spine-like, conspicuous, extending perpendicular to antennae. Length about half the length of pedicellus (Fig. 8A–B, H) 5

2. Legs relatively long (Fig. 3), hind tibia 6–10 times longer than wide and approximately two-thirds the tarsus length (Fig. 5A–C). Mouthparts long and slim in large specimens; penultimate article of maxillary palp 1.2–1.5 times longer than terminal article (Fig. 4G–I) and penultimate article of labial palp about 3 times longer than wide (Fig. 4F). Ovipositor short, barely surpassing apex of stylets IX, with 12 annuli (Fig. 5F) . . . . *T. texensis* species complex

\- Legs relatively short (Fig. 3), hind tibia 4–6 times longer than wide and approximately four-fifths the tarsus length (Figs. 6G

and 7D). Mouthparts short and robust; penultimate article of maxillary palp approximately equal in length to terminal article (Figs. 6E, 7C), and penultimate article of labial palp about 2 times longer than wide (Figs. 6F, 7B, 9B). Ovipositor short to long, with 12 or more annuli 3

3. Ovipositor relatively short, surpassing base of stylets IX by about 1.2–1.5 times the length of the stylets, with 12–14 annuli (similar to fig. 5F) . . . . *T. coahuilensis*

- Ovipositor long, surpassing base of stylets IX by more than 1.5 times the length of the stylets, gonapophysis with 14 or more annuli 4

4. Ovipositor long, surpassing base of stylets IX by 1.6–2.1 times the length of the stylets length. Gonapophysis with 14–15 annuli (Fig. 7F–G) . . . . *T. media*

- Ovipositor very long, surpassing base of stylets IX by 2.0–2.2 times the length of the stylets. Gonapophysis with 16–18 annuli (Fig. 6I) . . . . *T. aquilonalis*

5. Head with setae but without scales (Fig. 8A). Ovipositor very long, surpassing base of stylets IX by more than 2.0 times the length of the stylets (Fig. 8F) . . . . *T. occasus*

- Head with setae and scales (Fig. 8G). Ovipositor long, surpassing base of stylets IX by about 1.6–2 times their length (Fig. 8J) . . . . *T. capitesquameo*

An important question is, what is the total number of species within genus *Texoreddellia*? When conducting bioinventories, increased sampling efforts tend to yield increased numbers of species. The number of species recorded versus the number of samples collected follows an asymptotic curve, where the asymptote line is the actual number of species for a region. While the actual number of *Texoreddellia* species may never be learned, it appears that collecting efforts may have already reached the plateau level where most species have already been described, at least for the areas surveyed. It is noteworthy that despite the significant increase in sample size with respect to Espinasa & Giribet (2009), with an estimated 500 vials examined of the Texas Natural History Collections, not a single one had specimens that could unambiguously be assigned to a different species from those previously described. Undoubtedly there could be cryptic species with very similar morphology, or for which morphological differences are in characters other than those evaluated in this study. Nonetheless, the main conclusion of this study is that no previously undescribed phyletic groups or morphologically unique populations could be identified. This suggests that the total number of species in the area surveyed may not be much higher. One area that has the potential to yield new species is western Texas. Two species have been described from this area but collecting efforts and number of reported caves with nicoletiids are minimal when compared to those in Central Texas. Likewise, northern Mexico has received comparatively minor effort.

Biogeography. When Espinasa and Giribet (2009) described the biogeography of the genus, *T. aquilonalis, T. media, T. coahuilensis, T. capitesquameo*, and *T. occasus* appeared to have discrete geographical territories that followed a roughly east-to-west distribution in the order mentioned above. This study has shown that the first three species have broader distributions than previously assumed. While the trend may still persist to a limited degree, the main conclusion is that the ranges of these species overlap. Of particular relevance is the previous assumption that *T. aquilonalis* was restricted to Mexico, with the Rio Grande being a biogeographical barrier. Based on DNA and morphological results, this species also has a broad distribution in Texas.

The more highly troglomorphic species of *Texoreddellia* (*T. texensis* species complex) live only in total darkness and are usually found crawling on cave walls and floors in the presence of high humidity. The less troglomorphic species may be found in a wider variety of habitats, including both the dark and twilight zones. They may also occasionally be found under rocks. *Texoreddellia media* has been found in small crevices and voids encountered during construction, as well as in true caves.

Molecular results show that some species of *Texoreddellia* may disperse relatively quickly in evolutionary terms because populations inhabiting caves up to 200 km apart still have identical 16S rRNA haplotypes. This scenario is most easily explained by dispersal through the extensive network of cracks, fissures and smaller cavities of the epikarst. Also, several species have large, overlapping ranges. A consequence of fast dispersal and overlapping ranges is the possibility that the different species exist, at least in some caves, in sympatry. Ten caves for which we had specimens (6.5% of 153 caves analyzed) have been inhabited at one time or another by more than one *Texoreddellia* sp. This figure probably is an underrepresentation because most collections lacked a sample size large enough to detect the occurrence of more than one species.

Congeneric sympatry seems to be rare in Texas caves, with only four genera, including *Texoreddellia*, containing more than one species in a cave. The carabid beetle genus *Rhadine* LeConte is represented by species pairs in numerous caves along the Balcones Fault Zone (Barr, 1974; J.R. Reddell, unpublished data). In all shared caves, one species is highly troglomorphic and the other less troglomorphic. In the millipede genus *Speodesmus*

Loomis, a highly troglomorphic species and a less troglomorphic species occur in caves in southern Travis and northern Hays counties (Elliott, 1976). Two species of the pselaphine genus *Batrisodes* Reitter occupies one cave on Fort Hood in Bell County (Chandler et al., 2009). One is more troglomorphic than the other and they appear to be derived from different ancestors. Although one species pair of *Texoreddellia* (*T. texensis* and *T. media*) show the pattern of a more troglomorphic (*T. texensis*) and less troglomorphic (*T. media*) species occupying the same caves, we have found examples of species inhabiting the same caves where the two pairs have similar morphology. In most cases, the instances of sympatry between highly and less highly troglomorphic species is likely the result of different invasion events.

Acknowledgments

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